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Reprinted from  
*J. Neurophysiol.* 1966, 29  
pp. 530-544

# INTRACELLULAR RECORDING FROM EXTENSOR MOTONEURONS ACTIVATED ACROSS THE GAMMA LOOP<sup>1</sup>

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(Received for publication October 18, 1965)

BY RECORDING INTRACELLULARLY from cat motoneurons which have been activated across the gamma loop by tetani to the peripheral stump of the cut ventral root (see Fig. 1) it has been possible to elicit intrafusal stretch reflexes, in the sense that the spindle receptors have been stretched by contractions of their intrafusal musculature and hence excited. Preliminary mention of the experiments was made at a recent Nobel Symposium in Stockholm (25). Full description and analysis of these experiments is the purpose of this paper.

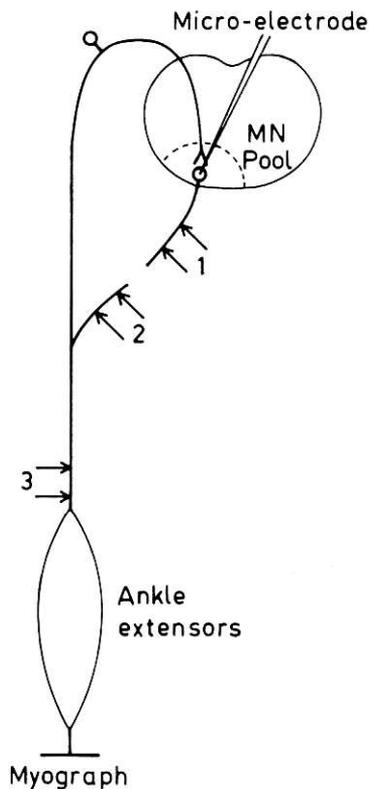
The intrafusal fibers, innervated by the gamma or fusimotor nerves, are of two kinds: *a*) large and long nuclear bag fibers and *b*) short and thin nuclear chain fibers (3, 6, 12, 13, 15, 48). The terminals of the primary receptors which deliver their impulses through the large so-called Ia afferent fibers, encircle the nuclear bag in an annulospiral fashion. They also send terminals to nuclear chain fibers. These large-size afferents have potent monosynaptic projections on their own motoneurons and to those of true synergists and produce autogenetic excitation (19, 24, 31, 38, 41). The large majority of the secondary end organs (group II afferents) lie on the nuclear chain fibers (5, 12, 13; see also 11). In the ankle-extensor motoneurons these afferents elicit autogenetic inhibition (33, 39). The net effect of the widespread intrafusal contractions elicited by electrical tetani to the whole root will therefore appear as some point of balance between these two antagonistic influences on the extensor motoneurons. Both types of receptor would, of course, pause during extrafusal contraction unless their high-threshold gamma fibers were activated so as to produce intrafusal contractions.

The third type of stretch receptor is the Golgi tendon organ which is best described as a recorder of contractile tension (24, 30, 36). The tendon organs in extensors are inhibitory to their own and to synergistic motoneurons (9, 24, 27, 30, 32, 46). Ventral root tetani are bound to produce tension and so the sum total of autogenetic effects on extensor motoneurons in our type of experiment will be  $E + I + I$ , the two inhibitory sources being the

<sup>1</sup> The authors are indebted to the Swedish Medical Research Council for a grant (Project No. 14 x-213-02A) in support of this work.

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FIG. 1. Schematic drawing of experimental arrangement. Microcapillary in single ventral horn cell of motoneuron pool belonging to ankle extensors gastrocnemius-soleus. Stimulating electrodes numbered 1, 2, and 3.



spindle secondaries and tendon organs. Calling excitation (E) + and inhibition (I) -, the algebraical sign of the sum as well as its numerical value can be altered by various experimental procedures to be described below.

In the classical reflexology of the Sherrington epoch one used to speak of "concealed" inhibition when an excitatory reflex was proved by various means to contain an inhibitory component. This was necessary as long as the effects of the end organs on motoneurons and the electrical responses of the latter to inhibitory or excitatory nerve impulses were unknown. Today, when, at least for leg extensors, we are reasonably familiar with the properties of the three types of receptor and the sign of their action on motoneurons, a good case can be made for regarding either excitation or inhibition to be concealed, depending upon the experimental procedures by which the algebraical sign of the sum and the numerical values of E or the two I's are altered to favor excitation or inhibition. The term "concealed" can have no other meaning than that the sum total of the influences playing upon the motoneurons, by various means, has been adjusted so as to favor E or I, de- or hyperpolarization, as the case may be.

Finally, it should be realized that when average reflex responses are supplanted by intracellular records from individual motoneurons it becomes possible to observe that the three types of receptor have projections of greatly varying relative density from cell to cell. On the whole, however, one would expect the monosynaptic excitatory component of the intrafusal stretch reflex to be dominant in our preparations because this reflex is "inevitable" while the polysynaptic effects of spindle secondaries and tendon organs are facultative, depending upon how the interneurons happened to be biased. Interneurons would be depressed in our cats which were anesthetized with pentobarbitone.

#### METHODS

The technique and procedures to be used below have been described in detail in three previous papers devoted to the study of the intracellular effects of stretch and contraction on motoneurons (27-29). The only significant changes introduced concern the stimulus parameters which are part of the presentation of the individual experiments. A brief summary of the experimental conditions should therefore suffice.

The only intact nerves of the leg used were the medial and lateral branches of the common popliteal which innervate the soleus and the two heads of the gastrocnemius. The opposite leg was wholly denervated. The ventral roots  $L_7$  and  $S_1$  were cut across in the middle on the experimental side so as to provide a central portion for eliciting antidromic field potentials and a peripheral stump for stimulation of the alpha and gamma fibers of the ankle extensors, generally by long-lasting tetani triggered by the sweep circuit at regular intervals. Conventional K-citrate or KCl microcapillaries were used for intracellular recording in combination with a circuit (2) for stimulating these neurons by currents injected from the tip of the microelectrode. The general arrangement of the experiment is schematically shown in Fig. 1.

It proved important to complete denervation of the animal in its frame while stimulating the peripheral stump of the root to be used, generally  $L_7$ , sometimes  $S_1$ , because only by direct observation was it possible to ensure that no muscles around hip and spine contracted to the root tetani.

With one exception (a decerebration) an initial dose of 35 mg/kg. of pentobarbitone was injected intraperitoneally. Additional amounts were given intravenously when slight movements of the animal showed them to be needed. Pneumothorax and artificial respiration were the rule. In all, 38 motoneurons were activated across the gamma loop.

An electrode on the cut popliteal nerve was also used (not illustrated in Fig. 1) because many popliteal ventral horn cells are synergists of the gastrocnemius-soleus motoneurons whose responses have provided the main data of this paper. Four popliteal synergists are included in this study.

Absolute values for initial passive tension are of little concern in the present type of experiment. Zero initial tension was equated to zero extension by observing within an accuracy of about 50 g. when the strain gauge of the myograph responded while the muscle was slowly extended millimeter by millimeter.

## RESULTS

### *General observations on loop activation*

If a gastrocnemius-soleus or popliteal synergist motoneuron could be fired by stretch of the ankle extensors it could also be fired by "loop activation," the latter term being used as an abbreviation for the results of stimulation of the peripheral stump of the cut ventral root by tetani at rates of the order of 250/sec. and at strengths reaching into the gamma range. In the last section of RESULTS the effect of stimulus frequency will be analyzed separately. If stretch failed to discharge the motoneuron and merely produced some depolarization with or without synaptic activation noise, injected subliminal or supraliminal outward currents sufficed to make both tests positive, stretch as well as loop activation, provided that the cell was in good condition and capable of firing repetitively. In several experiments the results were checked by the application of Xylocaine (Astra) to the peripheral nerve just above electrode 3 of Fig. 1. Cocaine has been shown (23, 44, 45) to paralyze small fibers before the large ones are blocked. Paralysis of gamma fibers by this means has proved to be a valuable analytical tool. It was introduced for this purpose by Matthews and Rushworth (43, 44) and has subsequently been employed a great deal.

Figure 2 serves for general orientation. At threshold strength for loop activation in light initial tension (Fig. 2A) there was one spike in record a. A 10 times stronger stimulus was used in record b. There was now a good discharge in spite of the larger contraction. Finally, the muscle was detached from the myograph in record c and the experiment repeated at the stimulus

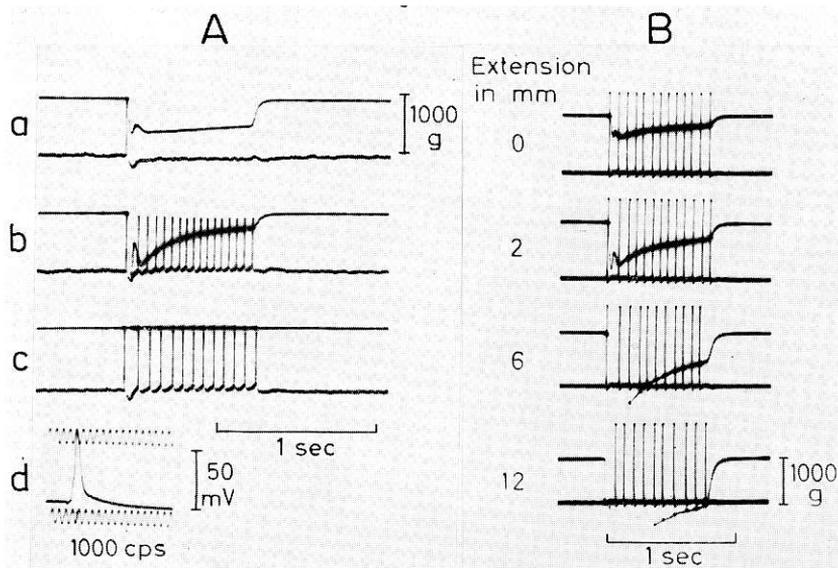


FIG. 2. Pentobarbitone cat. Simultaneous intracellular recording (below) from gastrocnemius-soleus motoneuron and isometric myogram (above) in response to stimulation of ventral root electrodes of Fig. 1 at a rate of 250/sec. *A*: d.-c. recording: a, light tension, stimulus strength 0.04 V.; b, increase of stimulus strength to 0.4 V.; c, same as b but with muscle detached from myograph; d, antidromic spike of the motoneuron used. *B*: a.-c. recording. Variation of extension of muscle as marked on the left against records.

strength used for b. This led to the expected reduction in discharge rate. Under fusimotor stimulation spindles have been shown to fire in slack muscle (21) but they will, of course, do better when properly extended (37, 40).

On the other hand, as contractile tension is increased step by step by extension of the muscle, most motoneurons will be more and more influenced by tendon organs delivering postsynaptic inhibition (24, 27, 30). For this particular motoneuron the effect of extension is shown in Fig. 2*B*. Alternating-current recording was used in this case. As the muscle was extended from zero to 12 mm. there occurred in the end a reduction of discharge rate during loop activation. This is the kind of effect that 30 years ago would have been interpreted as "concealed inhibition."

#### *Application of Xylocaine*

When applying Xylocaine to the muscle nerve in order to paralyze gamma efferents it is again necessary to recall that the net effect on the motoneurons in loop activation is a sum of E components and I components. In the present context this means that one may not have to paralyze all the gamma fibers before tension-sensitive inhibition overcomes excitation caused by loop activation. As to motor alphas and Ia afferents after application of cocaine, these have been found to show signs of paralysis at the same drug concentration (44).

The experiment of Fig. 3 illustrates on the left the effect of varying stimulus strength in loop activation. There was a large postsynaptic generator potential (EPSP), best visible at relative strength 1.0. Firing reached its maximum frequency at about four times this value. Somewhat later (on the right) Xylocaine was applied to the nerve after a control had been taken at near-maximum strength of stimulation. After 20 sec. only one spike remained of this discharge. The contraction was slightly increased in this

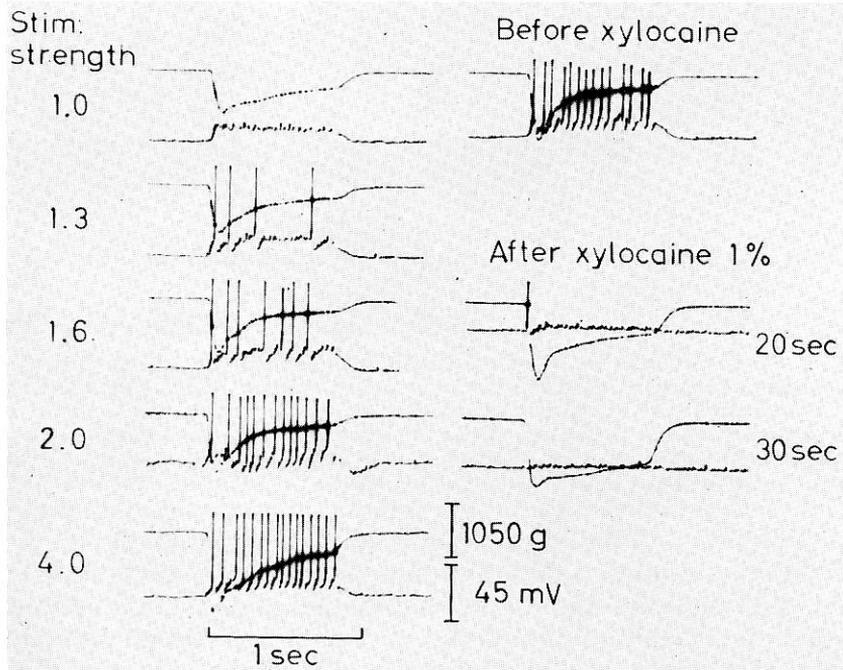


FIG. 3. Pentobarbitone cat. Direct-current recording from gastrocnemius-soleus motoneuron in response to stimulation at 500/sec. by electrodes 2 in Fig. 1 with myogram as in Fig. 2. Variation of relative stimulus strength marked against records on the left. On the right, control at arbitrary strength before application of 1% Xylocaine above nerve electrodes 3. Same strength used for the two records after application of Xylocaine, taken after 20 and 30 sec. respectively.

record, no doubt owing to the temporary rest given the muscle from stimulation while the drug was being applied. At this moment (20 sec.) an initial spike and a very small postsynaptic depolarization was all that was left of the large effect caused by loop activation with intact gamma supply (on the left). Ten seconds later paralysis had extended to the alpha motor fibers. (One is apt to use excessive doses of Xylocaine for fear of losing the cell before the experiment has been completed.)

It was suggested that the degree of completeness of gamma paralysis needed for quenching loop activation would depend chiefly upon the balance between excitation from spindle primaries and the amount of inhibition caused by tendon organs and spindle secondaries. The latter (group II affer-

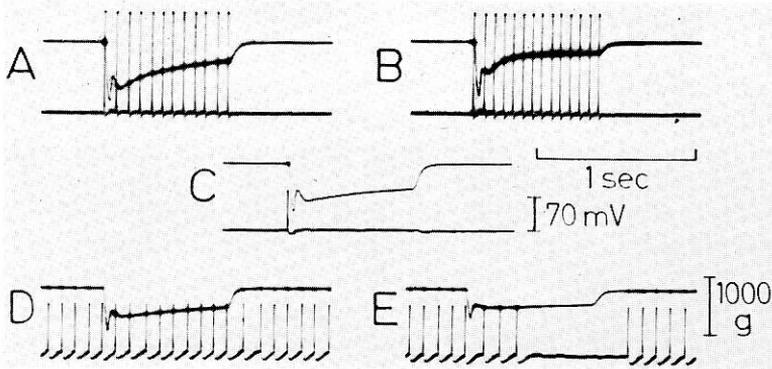
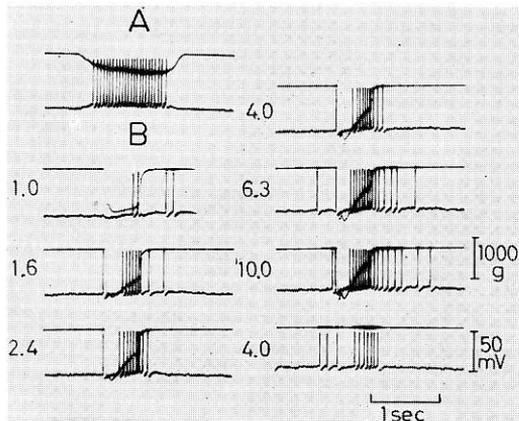


FIG. 4. Pentobarbitone cat. Recording from gastrocnemius-soleus motoneuron with myogram of ankle extensors as in Fig. 2. Rate of stimulation 250/sec. at electrodes 2. *A*: 10 mm. extension of muscle; stimulation strength around threshold for maximal extrafusal contraction. *B*: 2 mm. extension; stimulus strength doubled. Alternating-current recording used for *A* and *B*—then shifted to d.-c. recording and 2% Xylocaine applied above nerve electrodes 3. *C*: 14 sec. later; one spike of motoneuron and some depolarization to root stimulation remains. For *D* and *E* motoneuron was stimulated to discharge by injected current. Ventral root stimulation at electrodes 2 as in *B* and *C*, *D* at 30 sec. and *E* at 56 sec. after application of Xylocaine.

ents) may well be paralyzed at an early stage. Figure 4 shows how inhibition can be demonstrated in a motoneuron silenced after Xylocaine (27). *A* and *B* of this figure are two controls (a.-c. recording) with loop activation before Xylocaine. After *B*, recording was switched to the d.-c. amplifier and Xylocaine was applied to the nerve. In every other respect *C* was a repetition of *B*. Record *C* shows that 14 sec. after Xylocaine loop activation elicited only a single spike and a generator potential. The cell was thereafter fired with high regularity by transmembrane stimulation and root stimulation repeated after 30 (*D*) and 56 sec. (*E*), respectively, from the moment of application of Xylocaine. There was now inhibition in *E*, visible as a reduction of discharge rate in spite of the diminished contraction. Stimulation by spread of current to the root is excluded by the experiments of Figs. 3 and 4.

FIG. 5. Pentobarbitone cat. Direct-current records from gastrocnemius-soleus motoneuron together with myogram as in previous figures. All records at 5 mm. extension except bottom one on the right for which muscle was detached from myograph. *A*: manual stretch by pressing on string joining muscle and myograph. *B*: variations to changes of relative stimulus strength of tetani at rate of 500/sec., as marked against the records.



*Tonic and phasic responses to stretch*

Figure 5 presents records from a cell that had a good tonic response to stretch, as demonstrated in record A. Then followed loop activation at the relative stimulus strengths shown against the records. The last one (marked 4.0, bottom, on the right) which was intended for a control with muscle detached from the myograph came at a time when, unfortunately, the cell already had undergone some spontaneous depolarization, as seen from the diminished spike height. In the absence of an initial spike in record B at stimulus strength 1.0, the contraction caused some hyperpolarization followed by a depolarization, the latter indicating that loop activation gradually was gaining the upper hand. As stimulus strength was increased the excitatory effect became more prominent, no doubt owing to the mobilization of a greater number of gamma fibers. The strong high-frequency stimuli also caused Wedensky inhibition and, possibly, a local cathodal block. Since

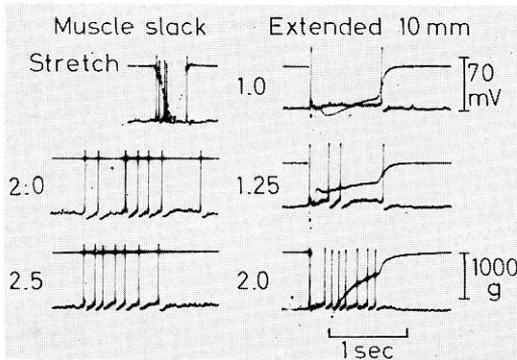


FIG. 6. Pentobarbitone cat. Direct-current records from gastrocnemius-soleus motoneuron with myograph as in previous figure. Stimulus rate at ventral root electrodes 2 was 500/sec. Relative stimulus strengths marked against the records. This cell responded phasically to stretch but tonically to loop activation.

these effects reduced contractile tension loop activation encountered less inhibition. The initial inhibition may well have been partly derived from spindle secondaries. This is suggested by the somewhat unreliable record taken with slack muscle (below, on the right).

Much the same maximum firing rates (Fig. 5) were reached by loop activation at higher stimulus strength in the records B as by stretch in the record A. Stretch was applied by pressing on the string joining muscle and myograph until firing rate was maximal. To extrafusal and intrafusal stretch, combined in this manner into an ordinary stretch reflex, no initial inhibition occurred (cf. records B). This is not surprising because the majority of tendon organs respond well only to active or contractile tension and they do so as long as tension is maintained (36). Some tendon organs have very low thresholds to contractile tension while many of them do not respond at all to passive stretch of any reasonable degree (36). Figure 5 also shows that loop activation at the higher stimulus strengths probably has stirred the spindles to discharge for sometime after stimulation.

Figure 6 is typical for a cell which merely responded to stretch by an initial burst of spikes (uppermost record, on the left). As will be seen, loop

activation at the relative stimulus strengths marked against the records was powerful enough to set up a tonic response which stretch alone had failed to engender. This was commonly noted in our experiments in which, owing to de-efferentation, gamma bias was low (21).

*Role of stimulus frequency: use of Flaxedil*

The stimulus frequencies in the records presented above have been 250 or 500/sec. The reason for using these high frequencies was the experimental finding that the optimum effects were obtained at around 250/sec. but that sometimes (an example below) an increase to the next frequency step, 500/sec., would cause improvement. Loop activation would, under the circumstances, be favored by 1) some fatigue of the extrafusal musculature caused by repetition of the tests, 2) a reduction of contractile tension owing to Wedensky inhibition, and 3) a measure of cathodal block under the stimulating electrode removing alpha fibers selectively. In the last instance these three factors operate by reduction of contractile tension and therefore need not be separated. Of greater importance for our understanding of the mode of action of stimulated intrafusal fibers is the question of whether these factors provide a sufficient explanation of what may be termed the frequency effect. The reply to this question follows from the experiments now to be described.

The gastrocnemius-soleus motoneuron of Fig. 7 was held for a long time (1 hour 10 min.) although it did undergo some slow depolarization owing to adjustments within the tissue. Consequently the electrode had to be reinserted twice. The second time (vertical row on the right of Fig. 7) refers to a complete repenetration from a wholly extracellular position and may therefore belong to an adjacent similar gastrocnemius-soleus cell. For the present purpose this is of little concern. Records 11 to 15 may just as well be regarded as an independent experiment.

When the experiment presented in Fig. 7 began, the height of the antidromic spike was 83 mV. It was fired by ventral root stimulation at 500/sec. at stimulus strength of 0.05 V. (record 1). In all successive records, from no. 2 onward, stimulus strength was at four times this value. The effect of loop activation in record 2 increased while the tension diminished. But in record 3, at rate 250/sec., the contraction was well enough maintained to prevent loop activation. The validity of this explanation is documented by records 4 and 5 which merely differ from records 2 and 3 by the spontaneous firing that the cell then initiated. Clearly, at 250/sec. there was powerful inhibition. Slight readjustment of the electrode followed after which it was decided to counteract inhibition by injecting depolarizing current into the motoneuron. This was done during records 6 to 10 while the effect of stimulus frequency on loop activation was being tested. In spite of the gradual depolarization that took place or, perhaps, partly because the latter also contributed to the same end, loop activation could now be carried down to a rate of 60/sec. with some spikes even at 30/sec.

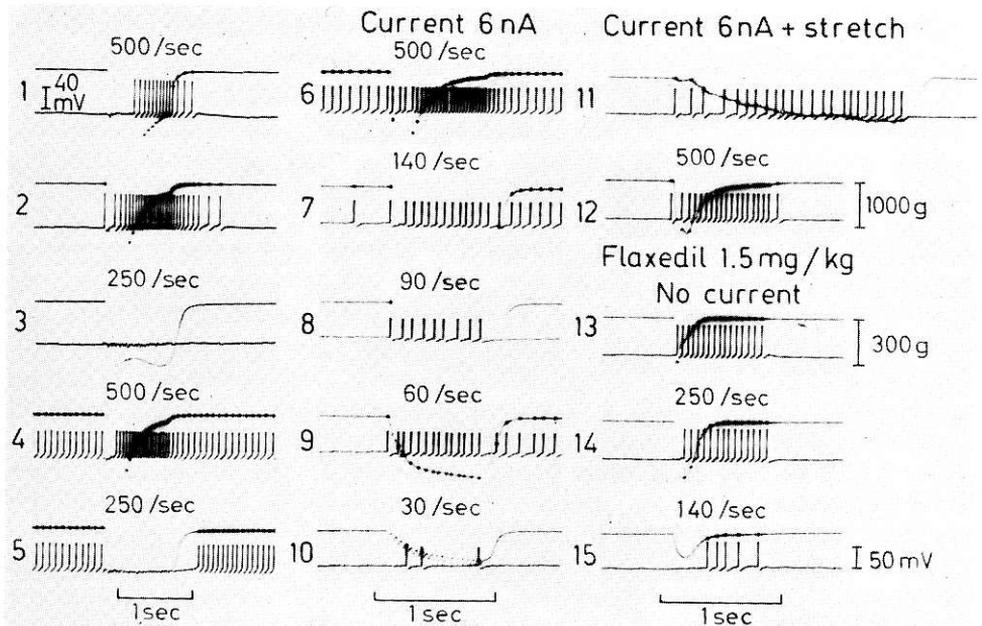
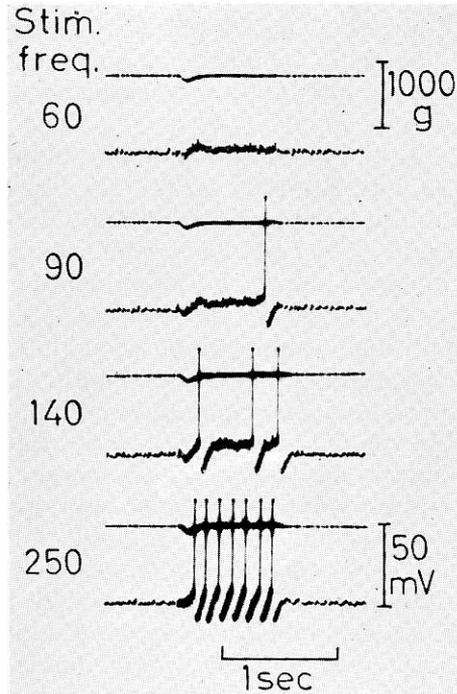


FIG. 7. Pentobarbitone cat. Intracellular d.-c. recording from gastrocnemius-soleus motoneuron. Stimulation at electrodes 2 with myogram as in previous figures. Rates of stimulation marked on the figure. Record 1 at stimulus strength 0.05 V., others at 0.4 V. Readjustment of recording electrode after record 5, reinsertion of it from extracellular position before record 11, which, exceptionally, refers to stretch of muscle and not to contraction. Applications of injected current (inside +) and of Flaxedil 1.5 mg/kg. iv as marked on the figure. Some myograph excursions were beyond range of measurement.

Reinsertion of the electrode for records 11 to 15 proved successful (or possibly it was a closely adjacent cell). This time the motoneuron could not be activated without the aid of injected current (6 nA.) but, this being supplied, it fired in records 11 and 12 to both stretch and contraction. The myograph sensitivity was then increased and a dose of 1.5 mg/kg. of Flaxedil injected in order to counteract contraction while the effect of the drug on the contraction was followed on the screen with the aid of single shocks to the ventral root. No sooner was the minimum reached than loop activation was started. It turned out that the cell could now be discharged at stimulus rate 500/sec. without the addition of transmembrane current from the microelectrode (record 13). Loop activation was also powerful enough to completely counteract the slight initial contraction (cf. the control record 12, before Flaxedil). The effect of stimulus frequency was tested. The lower limit was between 120 and 140/sec. (records 14 and 15).

Finally, in Fig. 8, a decerebrate animal was used which had received an initial dose of 1.5 mg/kg. of Flaxedil to which a little had been added cautiously until contraction became negligible. This can be done with maintained loop activation in extensors (9, 26) but in the ankle flexors a similar

FIG. 8. Decerebrate cat. Flaxedil in basic dose of 1.5 mg/kg. iv and thereafter more added cautiously while observing contraction disappear. Intracellular d.-c. recording from gastrocnemius-soleus motoneuron with simultaneous myogram as in previous figures. The variable rates of stimulation marked against the records in shocks per second. The membrane potential was 74 mV., the height of the antidromic spike 86 mV., and loop activation required maintained transmembrane stimulation by 6 nA.



state of differential paralysis is difficult to achieve (10). The experiment of Fig. 8 demonstrates that there is a favorable effect of stimulus frequency in loop activation despite virtual absence of contraction. Some depolarization is visible at a rate of 60/sec. but the full effect required a rate of 250/sec. There was no further increase at 500/sec.

A genuine effect of high stimulus frequencies as such could also be shown when the muscle was detached from the myograph in order to reduce contractile tension. High frequencies above 140/sec. would then fire the cells while low frequencies were ineffective. Thus the gamma loop in these experiments on activation of motoneurons behaves as if it could produce inhibition as well as excitation depending on stimulus frequency and, very clearly, the excitatory portion of the intrafusal apparatus displays properties quite different from those of its extrafusal counterpart. The intrafusal muscles for the excitatory path can build up and maintain long-lasting states of contraction and this takes place at rates of stimulation which the extrafusal system cannot endure. This is seen also in the favorable effect of stimulus duration because loop activation can go on for many seconds at the high stimulus rates used in this work, while the extrafusal contraction dwindles toward its vanishing point, especially if several such experiments are made in quick succession so as not to give the extrafusal system time for recovery.

#### DISCUSSION

The experiments have proved that the gamma loop of the ankle extensors is a motor route in its own right and that it can fire their motoneurons (together with synergists) not only overcoming the effect of unloading of the spindles by extrafusal contraction but also counteracting the inhibition from spindle secondaries and tendon organs, the latter being stimulated by active

contraction of the extrafusal musculature (24, 30, 36). Recent work on autogenetic inhibition in contracting ankle extensors shows it to be post-synaptic (27) and hence antagonized by depolarization produced by injected current, as in Fig. 7.

In the present case the whole fusimotor supply was electrically excited in a manner allowing for far less discrimination between types of gamma efferents than seems likely in real life. From the latter sphere come the experiments on normal respiration in which a large number of spindle primaries have been shown to fire optimally during contraction of the intercostal muscles in which they are situated (16, 20). This parallel with respiration shows that our findings are based upon some fundamental property of the intrafusal apparatus to the understanding of which they contribute information in spite of the unphysiological mode of stimulation. The salient point is that the data of the last section in RESULTS have demonstrated an effect of stimulus frequency as such, separable from what it achieves by influencing contractile tension in the complex manner demonstrated (and also discussed in connection with the presentation of the records).

There remains now to consider whether the inhibition from the spindle secondaries and the excitation from the primaries might be differentially sensitive to stimulus frequency. Actually, Smith (47), filming the movements of intrafusal muscles of transilluminated single spindles in the third lumbrical muscle of the rat's hind foot, has shown that there are two kinds of intrafusal fiber; one slow, the other rapidly contracting, to direct electrical stimulation. The rapidly twitching intrafusal fibers proved to belong to the small ones, the slowly contracting to the large ones (cf. INTRODUCTION). In a few cases identification of the slow fiber with the nuclear bag fiber proved possible.

Physiological evidence to the effect that in particular the secondaries can be "driven" at high frequencies (7, 14) is in full agreement with this observation that the nuclear chain intrafusal fibers are the fast, twitching kind while the nuclear bag fibers respond slowly. However, Kuffler, Hunt, and Quilliam (37) long ago reported that it sometimes proved possible also to "drive" primaries at stimulation rates of 50–180/sec. Since that time it has been demonstrated by Jansen and Matthews (34, 35) and Matthews (42) that there are separate static and dynamic gamma fibers and that "driving" of primaries is more easily obtained with the static nerve fibers activating the nuclear chain intrafusal fibers (17, 18, 42) on which the primaries, as stated, also have terminals. Recently Appelberg, Bessou, and Laporte (1) have shown that the secondaries, situated chiefly on the nuclear chain fibers, are controlled by static gamma fibers. One more interesting development in Laporte's laboratory (8) is that in recording from intrafusal fibers local changes of potential were found to occur on stimulation of nuclear bag fibers. This suggests that the conducted spikes, also seen in mammalian intrafusal fibers (8, 22), belong to the nuclear chain component.

At the recent Nobel Symposium in Stockholm (25, see especially Editor's summary) it was agreed upon by a number of well-known anatomists and

physiologists, active in this field, that the most plausible way of harmonizing these and other known observations on muscle spindles was to assign slow properties and a mechanism of excitation by local potentials to the nuclear bag fibers, fast properties, and conducted action potentials to the nuclear chain fibers. To this should be added that Crowe and Matthews (18) also report that most of their results could be explained on the idea that the nuclear bag fibers are the slow ones. In view of the considerable overlap of fusimotor fibers on spindles, a mechanism of local potential changes may well make the slow nuclear bag fibers build up summated states of contraction, highly dependent on stimulus frequency, while, at the end plates of the nuclear chain fibers, Wedensky inhibition possibly runs its course. There may also be considerable unloading of the nuclear chain fibers when the nuclear bag fibers are maximally contracted (7). It is doubtful whether maximal contractions can ever be obtained by stimulating single gamma fibers.

From these arguments follows the suggestion that, as long as rates of stimulation are used at which the majority of nuclear chain fibers go on twitching (i.e., being driven), each twitch will add its ration of inhibitory impulses running to the motoneuron in the group II afferents of the secondaries. At very high frequencies of stimulation the fused, slow, and cumulative contractions of the nuclear bag fibers will take over and maintain the excitatory impulses from the primaries in a state of dominance thereby producing the excitatory intrafusal stretch reflex that in this work has been activated across the gamma loop. In support of our explanation further arguments could be adduced from a fuller consideration of present data, which at the Symposium were summarized by Bessou and Laporte (8) and Smith (47), but more urgent at the moment seems to test it by experimentation, since Barker's histological data (4) demand less discrimination between the efferent mechanisms controlling primaries and secondaries than the physiological experiments (including our own) have made desirable in order to be consistent within their own sphere.

#### SUMMARY

1. Gastrocnemius-soleus motoneurons in the cat have been activated to discharge across the gamma loop by repetitive stimulation of the peripheral stump of a cut ventral root ( $L_7$  or  $S_1$ ) causing contractions of the extra- and intrafusal fibers of their muscles, careful attention having been given to denervation of all other muscles of the limb, hip, and pelvis (schematic diagram of experimental arrangement in Fig. 1). All results were obtained by conventional intracellular technique, used in parallel with the recording of isometric myograms from the ankle extensors.

2. Activation of the ankle-extensor motoneurons across the gamma loop could be prevented by local anesthetic blockade of their motor nerves at knee level and by intercepting the effect before the ensuing paralysis had reached the large motor alphas and the still larger afferents from the spindle primaries.

3. The inhibitory effect of tension receptors responding to contractile stress could be demonstrated by several experimental modifications including the use of Flaxedil for selective paralysis of the alpha end plates (see 9 and 26 for use of Flaxedil).

4. The extensor motoneurons could be fired across the gamma loop in the virtual absence of contraction (after Flaxedil).

5. For good activation of the motoneurons across the gamma loop it proved necessary to use stimulus frequencies above 140/sec., preferably 250–500/sec., though the lower limit could be reduced by depolarization of the motoneuron with the aid of current injected from the tip of the intracellular microcapillary.

6. After removal of contractile tension by Flaxedil the need for using high stimulus frequencies remained.

7. Thus the intrafusal muscle fibers carrying the excitatory receptor (spindle primaries) differed sharply in their properties from the extrafusal ones in their capacity for maintaining durable states of contraction at the high rates of stimulation used, and in proving to be far less fatigable with repetition of long-lasting tetani in rapid succession, both procedures severely depressing the end plates of the extrafusal ankle muscles.

8. The findings have been fitted into conclusions on the properties of intrafusal muscles on which preliminary agreement was reached at a recent symposium on the subject (25).

9. The experiments have demonstrated that the gamma loop is a motor route in its own right.

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